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Dicotyledonous leaf macrofossils from the latest Albian-earliest Cenomanian of the Eromanga Basin, Queensland, Australia.

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Abstract. Ten types of dicotyledonous angiosperm cuticle are described from bore core samples from the Early Cretaceous (latest Albian-earliest Cenomanian) of the Eromanga Basin, central Queensland. To date, these are the oldest organically preserved angiosperm macrofossils in Australia. Most of this material is found as small dispersed fragments, but two more intact lobed leaves were found. The affinities of some specimens are suggested to lie with the Chloranthaceae and Illiciales, and possibly the Platanaceae, but the rest are unknown. None of the cuticles show the paracytic stomatal arrangement which is common in extant plant families often regarded as 'primitive'. However, one of the cuticle forms exhibits a 'plastic,' variable form of subsidiary cell arrangment, which has previously been suggested as the most primitive condition. These angiosperms were a small component of an overwhelmingly gymnosperm (mostly conifer) dominated flora. They grew in clastic swamps, but may also have occured in coal swamps or sandy levees. The notably thin cuticle of some forms is consistent with an understory or deciduous habit.

Key words: angiosperm, Australia, Cretaceous, cuticle, stomate

Introduction

The first angiosperms appeared in Australia during the Barremian-early Aptian, and by the end of the Albian over 20 angiosperm(id) pollen types are known (Burger, 1990). Based on pollen records the angiosperms had originated somewhere distal to Australia by the Valanginian (Brenner and Bickoff, 1992; Brenner, 1996). The oldest angiosperm macrofossils in Australia are impressions from the Aptian of the Otway Basin in Victoria (Douglas, 1994). These impressions include a dicot identified as *Hydrocotylophyllum lusitanicum* Teixeira (Douglas, 1965). A further specimen, previously interpreted by Drinnan and Chambers (1986) as a possible fern, was later claimed as the world's oldest flower (Taylor and Hickey, 1990; although this distinction is now claimed by Late Jurassic material from China, Sun *et al.* 1998). The Australian Late Cretaceous angiosperm macrofossil record is very poor, probably due to a lack of outcrop. Scattered impressions and some cuticular debris are known from drill core material from the later part of the Victorian Cretaceous but have not been formally documented. McLoughlin *et al.* (1995) illustrated several dicotyledonous leaf impressions of probable Cenomanian age from the Eromanga Basin of central Queensland. Their material came from surface outcrop of the Winton Formation (Vine and Day, 1965; Exon and Senior, 1976) which has undergone considerable weathering. Below this zone, in samples obtained from bore cores for this study, weathering and lithification have been minimal and anatomical details (including cuticle) of fossil plants are preserved (Pole, 1999; Pole and Douglas, 1999). This material has been dated palynologically as close to the Albian-Cenomanian boundary (Dettmann and Playford, 1969; Helby *et al.*, 1987; Dettmann *et al.*, 1992). The purpose of this paper is to document the dicotyledonous macrofossils from bore core samples of the Eromanga Basin.

Dicotyledon leaf fragments were recognised by having net venation comprising more than one order, or thickness of veins, and confirmed with epidermal characters. Angiosperm cuticle was recognised partly by its robustness, i. e. it is strong enough to survive processing and handling. This eliminates from consideration the ferns, which in any case, are generally distinct on morphological characters (van Cotthem, 1970a). The Early Cretaceous fern *Weichselia*, which does have relatively thick cuticle, is singularly unique in morphology. *Weichselia* is more similar to *Equisetum* and some gymnosperms (Alvin, 1974), having relatively large, randomly oriented guard cells, which are not sunken or over arched by subsidiary cells, but have an outer stomatal ledge. On these criteria there is little else in the Early Cretaceous which could be confused as dicotyledonous, with the possible exception of the Caytoniales. Harris

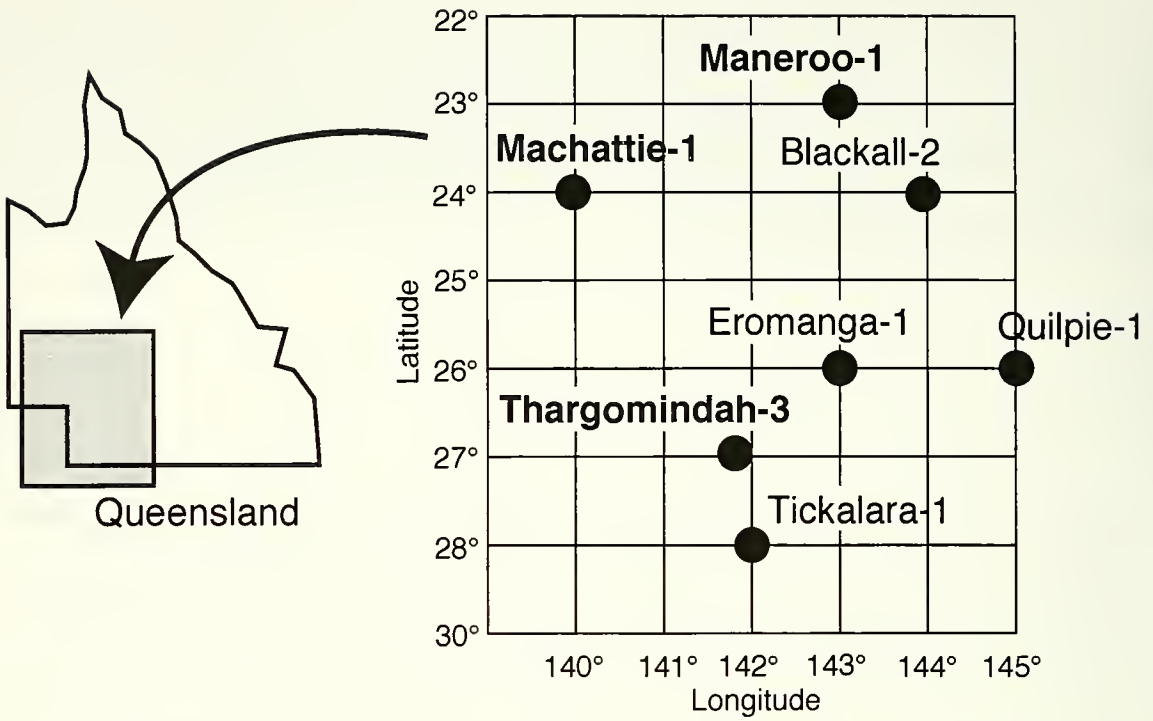

Figure 1. Locality map. The position of the study area within Queensland, Australia, is shown at left, and the position of all drill cores sampled within the study area is shown at right. Names of drill cores which provided dicotyledonous cuticle are in bold.

(1940) described *Sagenopteris* cuticle which had guard cells, apparently (according to his sketch) without outer stomatal ledges, no distinct subsidiary cells, and trichomes with basal cells. A cuticle type from the Winton Formation with possible affinities to the Caytoniales is described in Pole and Douglas (1999). Monocotyledon cuticle is generally distinct and is dicussed in Pole (1999).

My separation of fossil cuticles into morphological groups is based on my experience with the cuticle of extant plants. In my opinion the forms described below represent individual species.

Materials and methods

Seven bore cores were selected from the Eromanga Basin in central Queensland (Figure 1); GSQ Blackall-1, GSQ Eromanga-1, GSQ Quilpie-1, GSQ Machattie-1, GSQ Maneroo-1, GSQ Thargominda-3, and GSQ Tickalara-1 (these cores are stored in a Geological Survey of Queensland (GSQ) warehouse at Zillmere, Brisbane). Each core penetrates fluvial sediment of the Winton Formation and the underlying marine sediment of the Allaru and Mackunda Formations. Samples of approximately 5 cm^3 each were selected for macrofossil preparation, based on a visual appraisal of the sediment. Each sample was numbered consecutively and prefixed with the first three letters of the bore core name. Stratigraphic details of samples which contained dicotyledonous macrofossils are given as

Table 1. Stratigraphic details of samples with dicotyledonous macrofossils.

SAMPLE	DEPTH/M	FORMATION
MAC-3	155.44	Winton
MAC-7	193.49	Winton
MAC-11	319.7	Mackunda
MAN-6	28.8	Winton
MAN-7	29.4	Winton
MAN-8	29.7	Winton
MAN-9	29.8	Winton
MAN-11	29.95	Winton
MAN-12	30.0	Winton
MAN-20	39.4	Winton
MAN-22	42.0	Winton
MAN-23	42.3	Winton
MAN-28	80.4	Winton
MAN-30	86.8	Winton
MAN-34	161.6	Mackunda
MAN-42	326.4	Mackunda
THA-24	218.0	Winton
THA-32	240.3	Winton
THA-41	292.3	Winton
THA-47	313.3	Winton

Table 1 (details of all samples are given in Pole and Douglas, 1999). Carbonaceous muds were preferred, sands were avoided unless they contained prominent carbonaceous horizons, and lignites were also generally avoided (previous experience and some tests indicated these usually do not preserve cuticle). Carbonaceous material was sparse in the marine sediment. Only two nearly intact leaves were recognised in hand specimen, the rest were small fragments of leaf lamina exhibiting some net venation or cuticle. In total, 235 samples were taken. Samples were numbered consecutively from the top of the core and given a prefix of the first three letters of the core name.

Most of the sample was processed for cuticle, leaving a small amount as a voucher specimen. Samples usually broke down into a sludge with the addition of warm water, but sometimes addition of a little hydrogen peroxide was needed. Sludge was washed through 500 and 125 µm mesh sieves, with most workable cuticle being retained on the 500 µm. Further clearing of cuticle involved increasing concentrations of warm peroxide. This treatment was controlled so that fragments retained veins or resin glands. Further clearing so that only cuticle remained used aqueous chromium trioxide. Any adhering silicates were removed with hydrofluoric acid.

Samples were scanned under a binocular microscope, the dominant floristic components were estimated, and specimens were removed with tweezers for transmitted light microscopy (TLM) or (when sufficient extra material was available) scanning electron microscopy (SEM). Crystal Violet was used to stain when necessary.

There are insufficient data for the dicotyledonous cuticles to formally diagnose new taxa and an informal system of nomenclature is used. Macrofossils and slides are catalogued with the prefix 'SL' and are stored in the Department of Botany, University of Queensland. Specimens mounted on Electron Microscope stubs are catalogued with the prefix 'S'. Specimens for TLM viewing were mounted on microscope slides with glycerine jelly, and those for SEM viewing on stubs with double-sided tape and coated with gold.

Results

Dicotyledon sp. A

Figures 2, 3

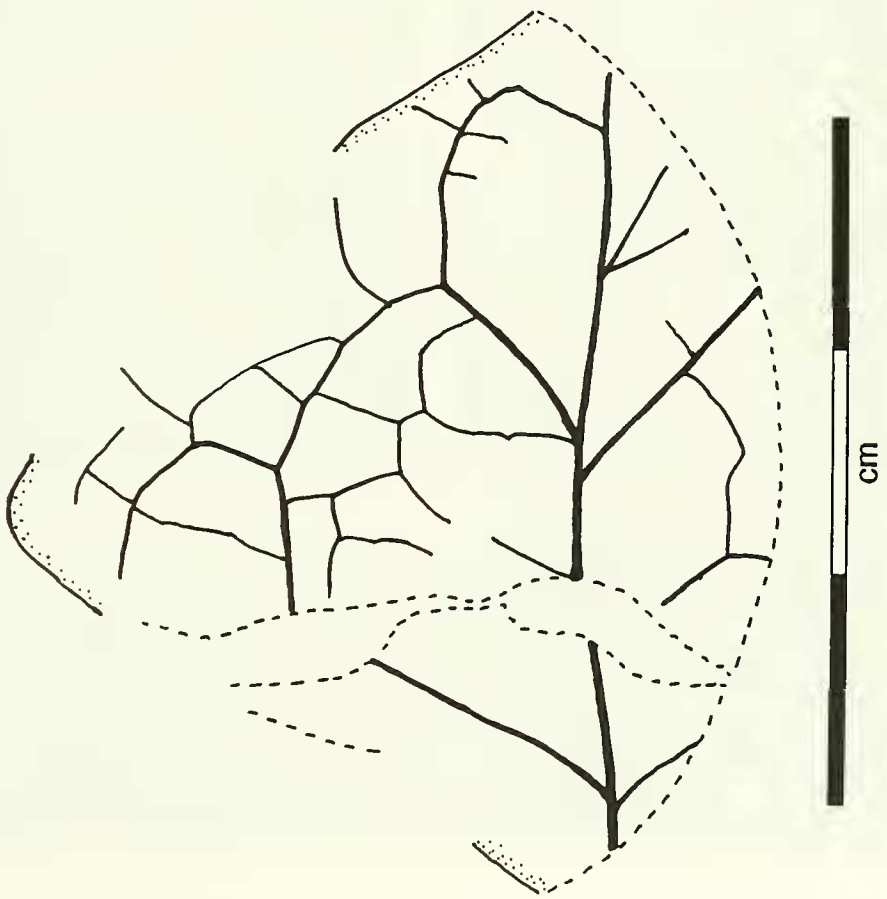

Figure 2. Dicotyledon sp. A, SL797. Line drawing of the only near-intact dicotyledon fossil found. Stipple = margin, dashes = broken lamina. See Fig. 3 for photographs.

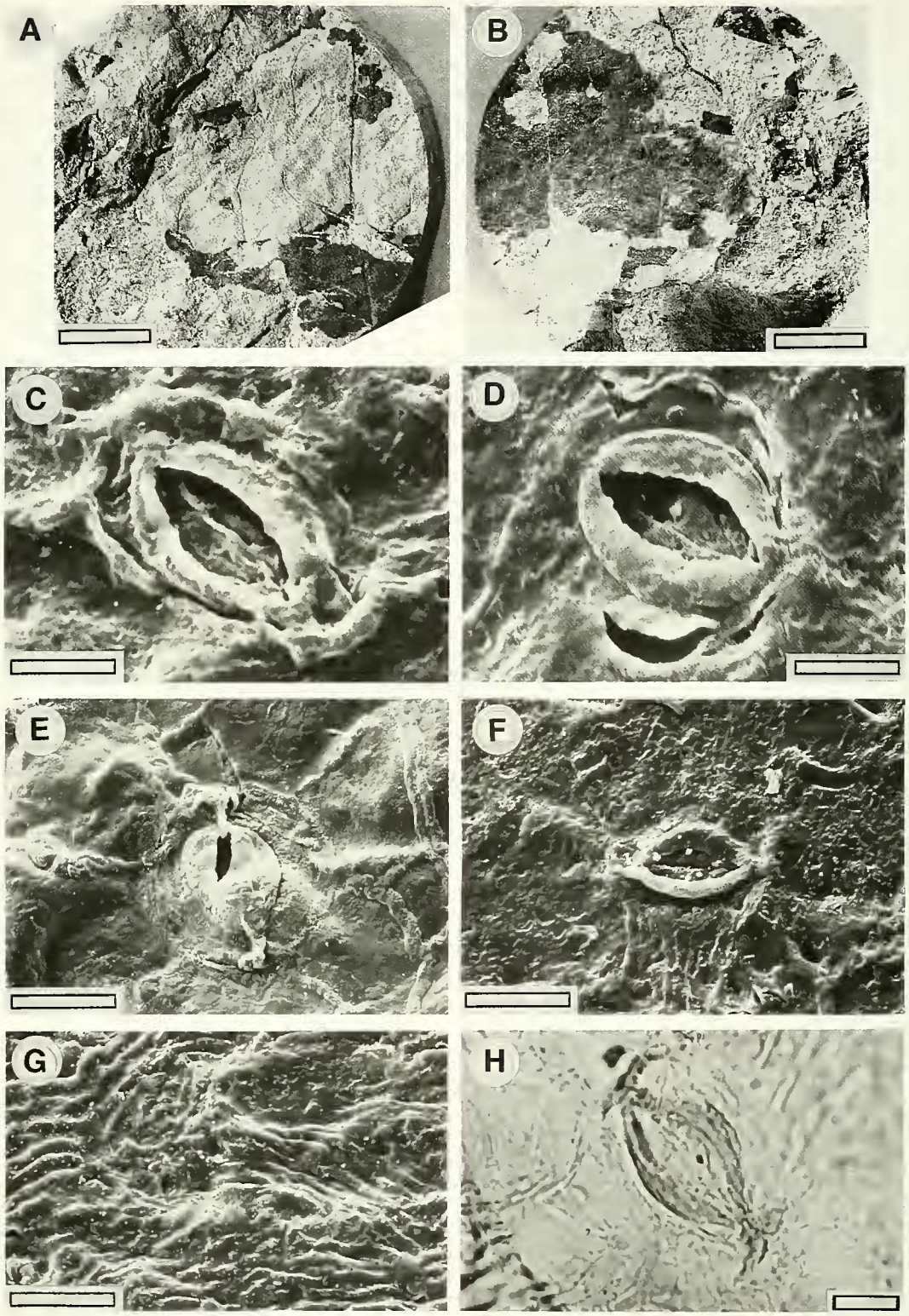

Figure 3. Dicotyledon sp. A. **A**. Intact leaf on bedding surface of drill core sample, SL797, scale: 1 cm. **B**. Counterpart of SL797, scale: 1 mm. **C**. SEM of outer surface of stomate, S761, scale: 10 µm. **D**. SEM of outer surface of stomate, S763, scale: 10 µm. **E**. SEM of inner surface of stomate, S763, scale: 20 µm. **F**. SEM of outer surface of stoma showing ridges extending from lateral margin, S761, scale: 20 µm. **G**. SEM of outer upper leaf surface showing ridges, S773, scale: 20 µm. **H**. TLM of stomate, SL678, scale: 10 µm.

Reference specimen.—SL797 (almost intact leaf on bedding surface, MAN-11).

Referred specimen and occurrence.—SL996; MAC-3 (dispersed cuticle).

Description.—Leaf lobed, length about 40 mm, width about 50 mm (midrib-margin 24 mm), hypostomatic; on abaxial surface stomatal orientation random; outline of guard cell pair ovate, outer stomatal ledge broad, T-piece thickenings at poles prominent; subsidiary cells not visible under TLM, under SEM typically 6 isodiametric contact cells visible; cuticle very thin, epidermal cell flanges not visible under TLM; on surface ridges of cuticle sometimes present over outer walls of guard cells, also bands of fine ridges prominent, extending laterally from guard cells; glabrous; adaxial surface epidermal cell flanges visible under TLM, isodiametric, polygonal, straight-walled; finely and evenly ridged on surface; glabrous.

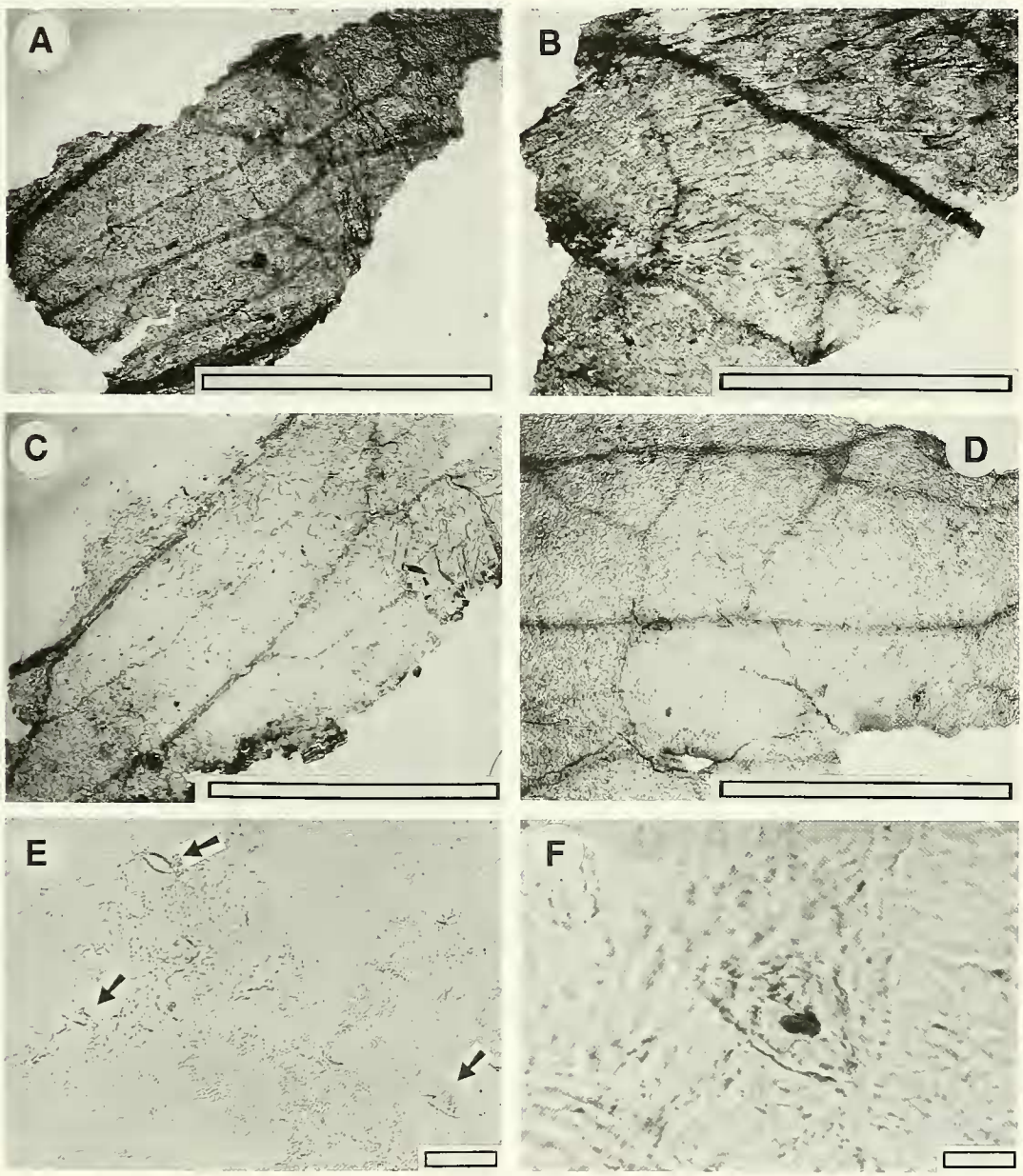

Figure 4. Dicotyledon sp. B. **A**–**D**. TLMs of leaf fragments with net-venation, scale: 1 mm. **A**. SL776. **B**. SL777. **C**. SL774. **D**. SL773. **E**. TLM of cuticle showing widely separated, aligned stomata (arrowed), SL787, scale: 50 µm. **F**. TLM detail of single stomate, note narrow, elliptical rim, SL787, scale: 10 µm.

Dicotyledon sp. B

Figure 4

Reference specimen.—SL787 (dispersed cuticle, MAN-23).

Referred specimens and occurrence.—SL997, MAN-9; SL774, MAN-11; SL773, MAN-20; SL771, MAN-22; SL776, SL777, MAN-23; SL788, MAN-34.

Description.—Leaf shape unknown, small fragments of lamina exhibit net-venation; stomata scattered, infrequent, visible under TLM as very thin, aligned (at least over small areas), elliptical, outer stomatal ledges; cuticle otherwise very thin, no clearly distinguished subsidiary cells, epidermal cell flanges generally not visible, isodiametric, smooth,

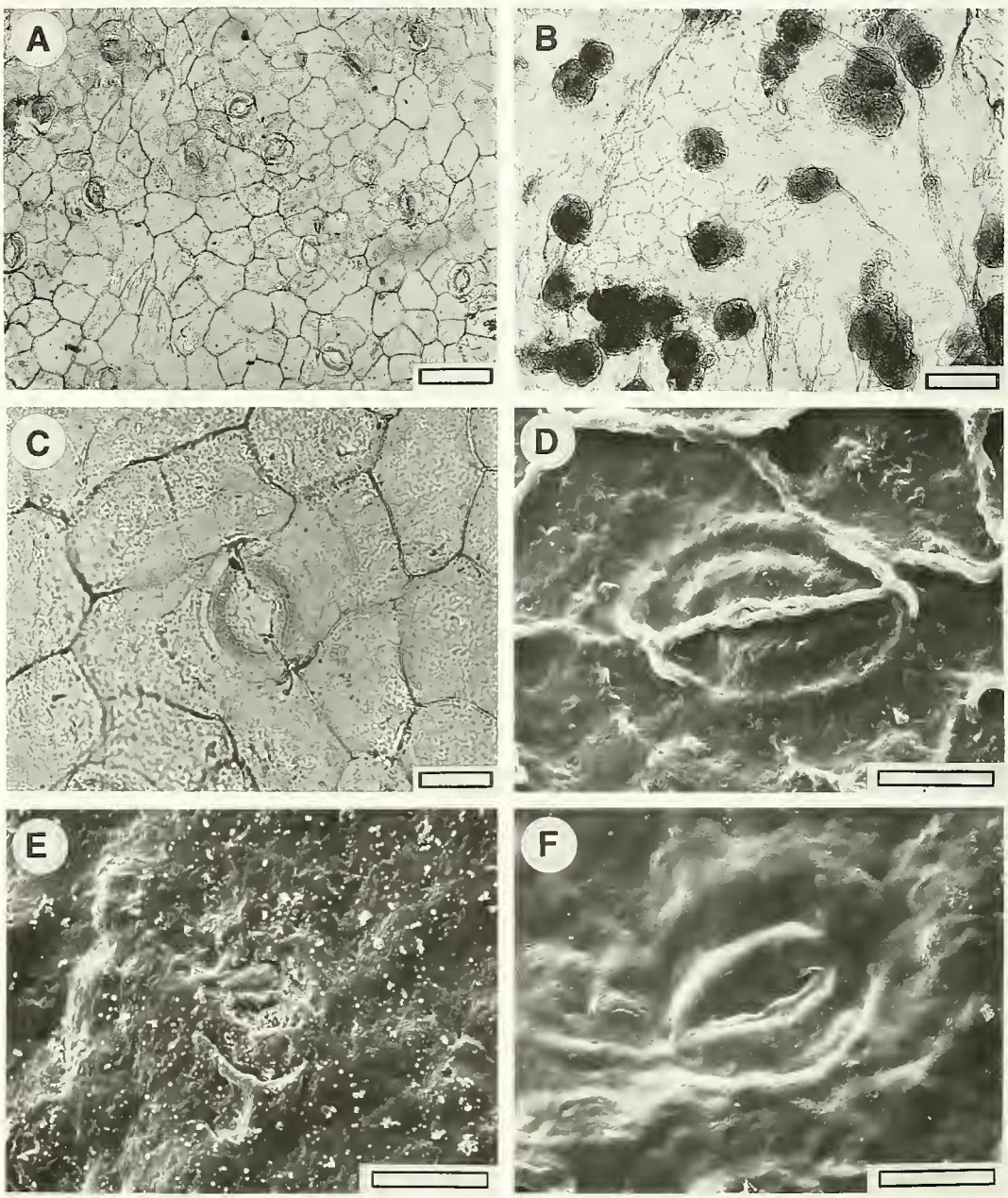

Figure 5. Dicotyledon sp. C. **A**. TLM, SL738, scale: 100 µm. **B**. TLM with numerous dark resin bodies still attached, SL735, scale: 100 µm. **C**. TLM of single stomate, SL738, scale: 25 µm. **D**. SEM of inner surface of single stomate, note T-piece thickening, S765, scale: 20 µm. **E**. SEM of outer surface of single stomate, S759, scale: 20 µm. **F**. SEM of outer surface of single stomate, S765, scale: 20 µm.

slightly thicker over veins; glabrous.

Dicotyledon sp. C

Figure 5

Reference specimen.—SL738 (dispersed cuticle, MAN-30).

Referred specimens and occurrence.—SL731, MAN-6; S760, MAN-7; SL733, MAN-8; S765, MAN-9; S759, MAN-11; SL735, MAN-12; SL739, MAN-42; SL676, THA-32.

Description.—Stomatal orientation random, outer stomatal ledges broad; distinct, thin T-piece thickenings at guard cell poles; peristomatal thickening sometimes present; no clear or consistent subsidiary cell arrangement but lateral contact cells often divided tangentially to give irregular-shaped subsidiary cells; normal epidermal cells polygonal, smooth; major veins (midrib?) visible as more elongate, rectangular epidermal cells; outer cuticular surface smooth; typically glabrous but sparse poral trichome bases sometimes present; resin bodies from within leaf lamina often adhering to cuticle (e. g. SL735).

Note.—The resin bodies are similar to those widespread throughout the extant magnoliids (Metcalfe, 1987; pers. obs.).

Dicotyledon sp. D

Figure 6

Reference specimen.—SL676 (dispersed cuticle, THA-32)

Referred specimens and occurrence.—SL895, MAC-7; SL677, THA-41

Description.—Stomatal distribution over leaf unknown; stomata randomly oriented; guard cell pair outline ovate, central portion covered by broad outer stomatal ledge; T-piece thickenings present at guard cell poles; subsidiary cell pattern variable, polar and lateral subsidiary cells typically recognisable, but sometimes not; lateral subsidiary cells present in up to three layers (including the hexacytic arrangement of van Cotthem, 1970b), apparently formed by

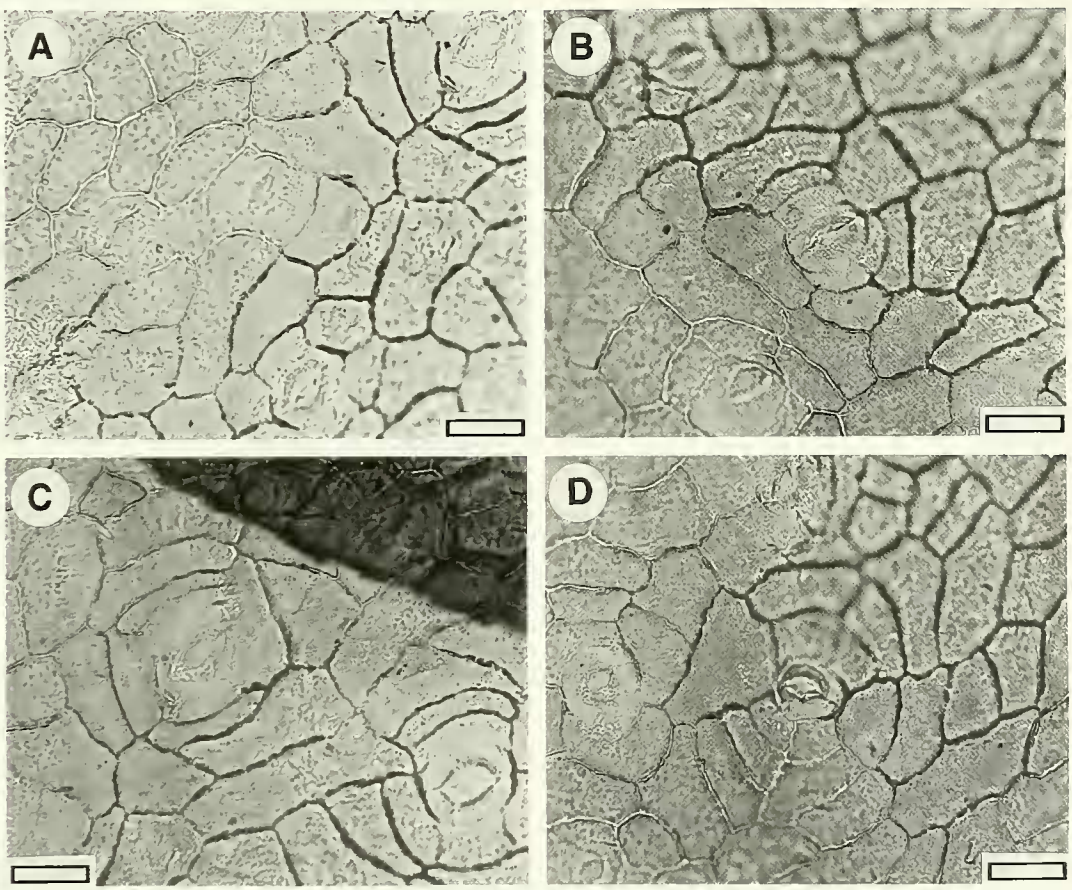

Figure 6. Dicotyledon sp. D, all SL676, TLMs of stomata of varying type, scale: 25 µm. **A**. Stomata with single lateral subsidiary cells on either side, some have divided radially. **B**. Stoma with 3 lateral subsidiary cells on one side, and two on the other which have both divided radially. **C**. Stomata with two lateral subsidiary cells. **D**. Stoma with six lateral subsidiary cells on one side.

elongate, tangential divisions of contact cells, sometimes also radially divided (i. e. giving six lateral subsidiary cells on one side of stoma); polar subsidiary cells irregular (probably just unmodified contact cells) or sometimes elongate, forming from tangential division of contact cell; veins not reflected in epidermal cells; glabrous.

Dicotyledon sp. E

Figure 7

Reference specimen.—SL772 (only specimen, small leaf with apex and base missing, two teeth present, MAN-34).

Description.—Leaf toothed or lobed, preserved lamina length 6 mm, up to 4 mm wide, teeth/lobes 0.8 mm wide and high; first order venation externodromous; tooth vascularisation central; stomata visible only as thin, elliptical outer stomatal ledges; aligned with midrib when close, or aligned with lateral venation further away; resin bodies numerous within lamina.

Dicotyledon sp. F

Figure 8

Reference specimen.—SL678 (dispersed cuticle, only specimen, THA-24).

Description.—Stomatal distribution over leaf unknown; stomata randomly oriented; outer stomatal ledges prominent, elliptical, sometimes narrowing abruptly before poles; prominent T-piece thickenings at stomatal poles; subsidiary cells not visible; cuticle very thin, epidermal cell flanges not visible in TLM, faint under SEM; outer epidermal surface ornamented by swirling bands of fine ridges sometimes starting at right angles from lateral subsidiary cells, but also with no consistent orientation to stomates; sometimes peristomal ridges present along edges of guard cells.

Note.—The general appearance of the cuticle, particularly the surface ornamentation, appearance of the outer stomatal ledge, and the prominent T-piece thickenings are comparable with two extant genera of the Illiciales, *Kadsura* (Schisandraceae; cf. fig. 24F Metcalfe, 1987) and *Illicium* (Illiciaceae; cf. fig. 22B Metcalfe, 1987), suggesting a relationship with this order. The same features are comparable with *Eucalyptophyllum oblongifolium* Fontaine from the Potomac Group, which was suggested by Upchurch (1984, p. 544 and cf. his figure 7) to represent "an extinct group of at least ordinal rank... that is related in some way to Chloranthaceae and Illiciales."

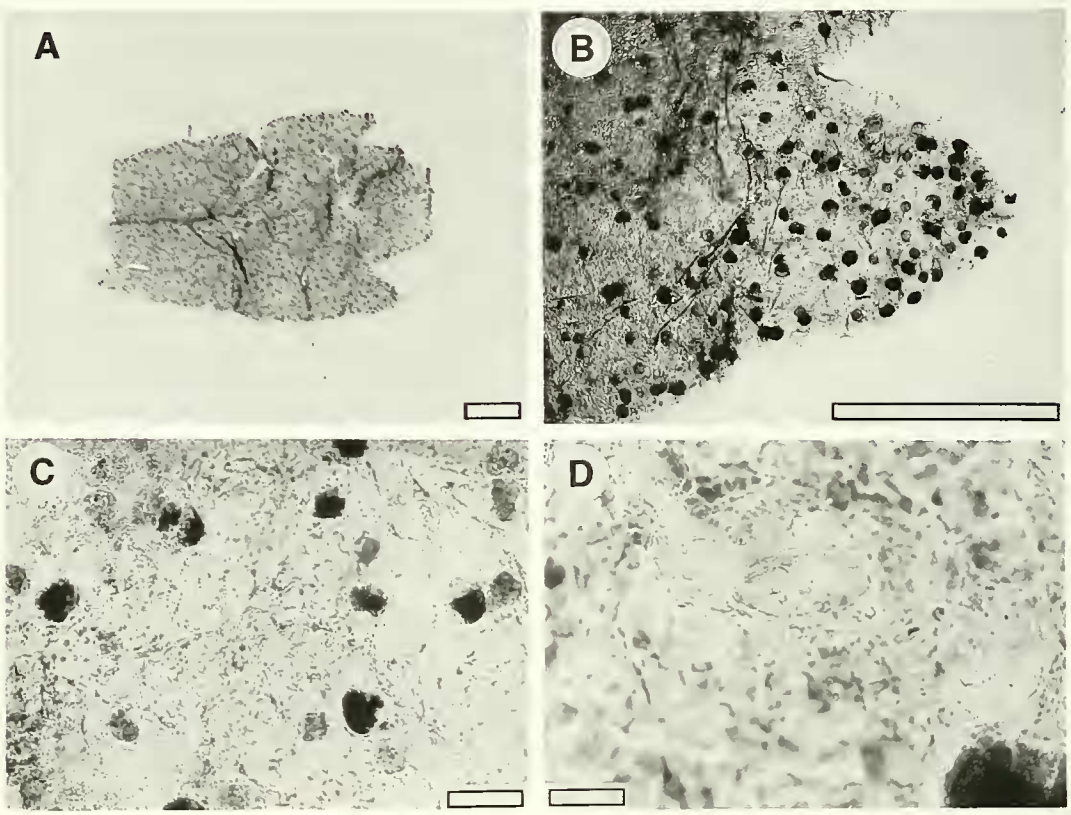

Figure 7. Dicotyledon sp. E, all SL772. **A**. TLM of complete specimen, note teeth and broken apex, scale: 1 mm. **B**. TLM detail of tooth showing numerous resin bodies, scale: 1 mm. **C**. TLM detail showing stoma (arrowed) and resin bodies, scale: 100 µm. **D**. TLM detail of single stomate, scale: 25 µm.

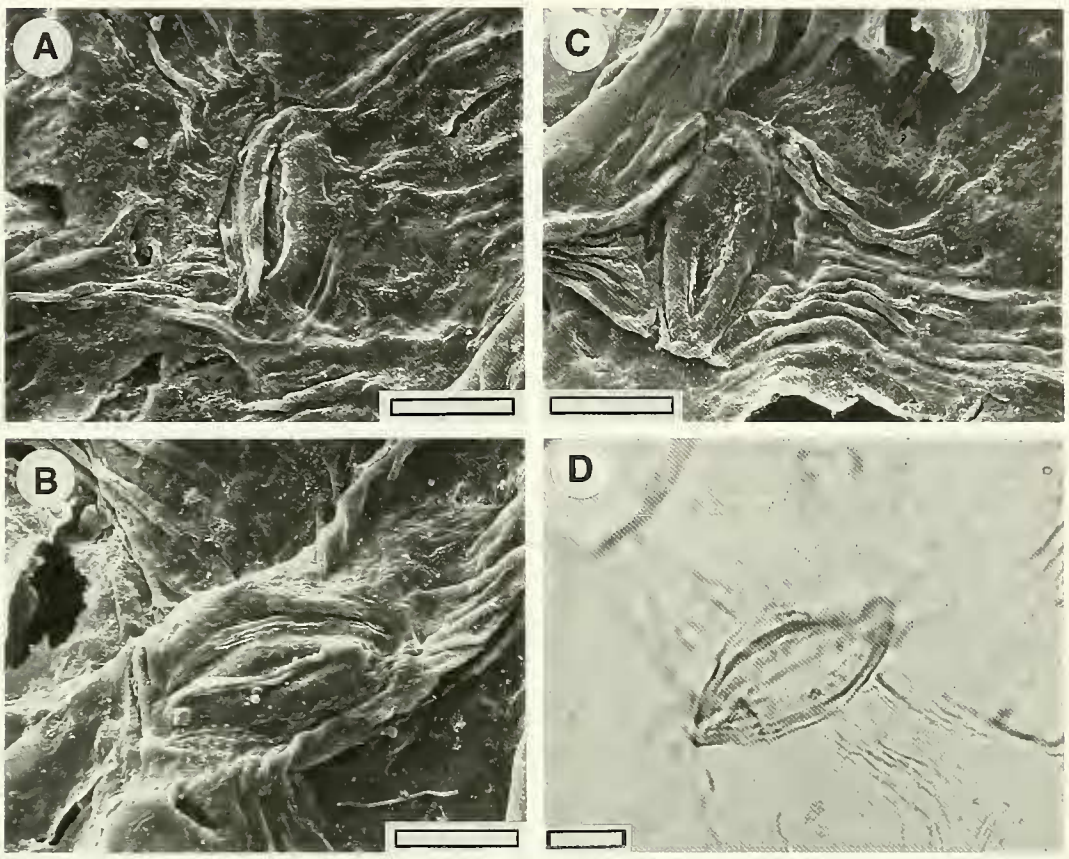

Figure 8. Dicotyledon sp. F. **A**–**C**. SEMs of outer surface of single stomate, all S764, scale: 20 µm. **D**. TLM of outer surface of single stomate, SL768, scale: 10 µm.

Dicotyledon sp. G

Figure 9

Reference specimen. — SL894 (dispersed cuticle, only specimen, MAC-11).

Description. — Stomatal distribution over leaf unknown; stomata randomly oriented; normal stomata sunken under and occluded by frilled, radiating rim of cuticle; giant stomata common, exposed, with thin, elliptical, outer stomatal ledge, surrounded by low tangentially oriented ridges; major veins only reflected in epidermal cells; glabrous.

Dicotyledon sp. H

Figure 10A, B

Reference specimen. — SL987 (dispersed cuticle, only specimen, MAC-3).

Description. — Stomatal distribution over leaf unknown; stomata randomly oriented; normal stomata dense; outer stomatal ledge broad, narrowing at poles, not extending full length of guard cells; moderate T-piece thickenings at stomatal poles; peristomal thickenings sometimes present; giant stomata present; no distinct subsidiary cells; contact cells of separate stomata often abut, sometimes shared; outer stomatal ledge wide; normal epidermal cell shape irregular, rounded, generally slightly elongate; fine ridges on outer surface of cuticle oriented parallel to stomatal pore; major veins reflected in more rectangular, slightly papillate epidermal cells; glabrous.

Dicotyledon sp. I

Figure 10C, D

Reference specimen. — SL737 (only specimen, poorly preserved leaf fragment near apex, bases of teeth present, MAN-28).

Description.—Leaf margin with small teeth; stomatal distribution over leaf hypostomatic; stomata randomly oriented; guard cell pair outline ovate; outer stomatal ledge narrow, not extending full length of guard cells; no obvious subsidiary cells; epidermal cell flanges prominent; normal outline polygonal, isodiametric; midrib reflected in epidermal cells.

Dicotyledon sp. J

Figure 10E, F

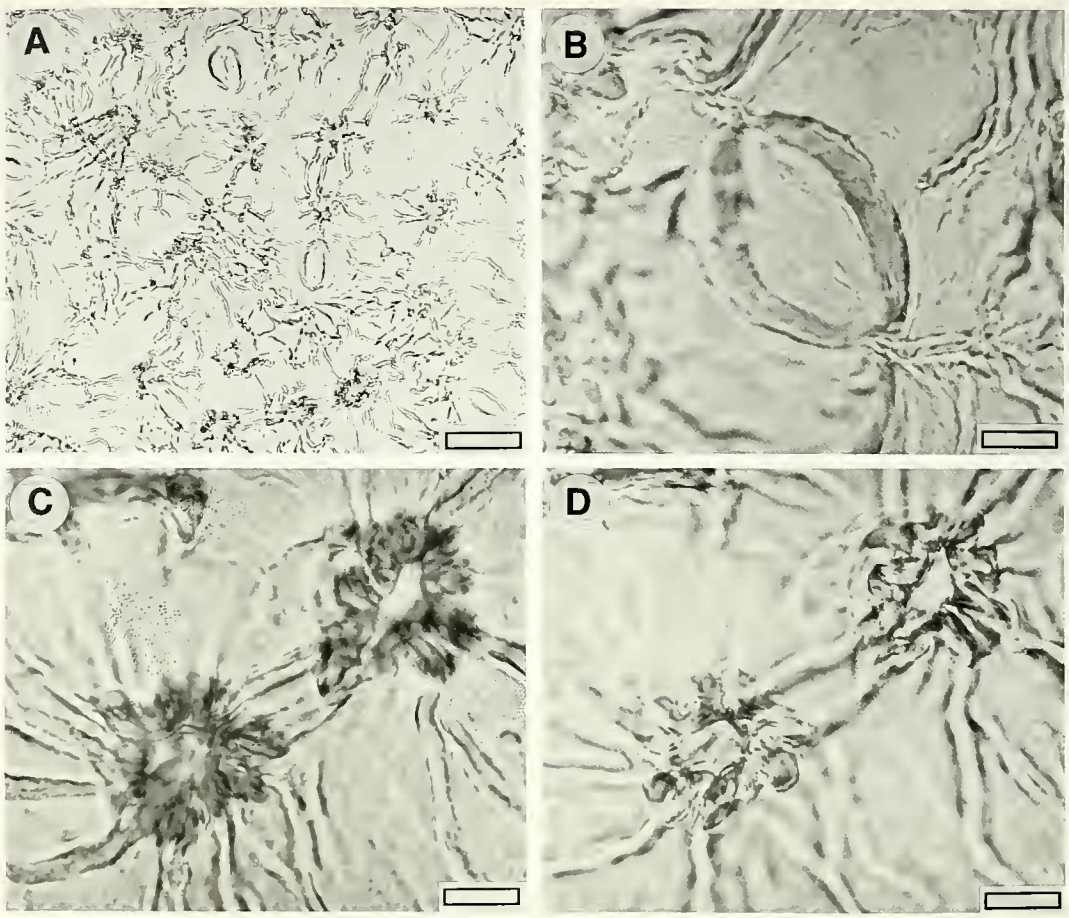

Figure 9. Dicotyledon sp. G, all SL894. **A**. TLM showing exposed giant stomata and normal stomata obscured by cuticle ridges, scale: 50 µm. **B**. TLM detail of giant stomate, scale: 10 µm. **C, D**. TLM of two normal stomates. **C**. Lower focus. **D**. Higher focus, scale: 10 µm.

Reference specimen. — SL679 (dispersed cuticle, only specimen, THA-47).

Description. — Stomatal distribution over leaf hypostomatic; on abaxial surface stomata generally aligned but some oblique, striations aligned with stomates, elliptical, thickened outer stomatal ledge, epidermal cell flanges not visible under TLM; glabrous; adaxial surface also with parallel striations, glabrous.

Identification

Worldwide, most described angiosperm leaf fossils of Albian-Cenomanian age are impressions only, lacking cuticle. However, in this study, although cuticular preservation is good, most material is found as small, dispersed fragments in amongst a large amount of coniferous material (the chances of a bore core sampling a complete leaf are slim). This situation is frustrating, as a combination of gross leaf morphology and venation combined with anatomical detail would be a great help in identification. Nevertheless, these are the best preserved angiosperms from the Australian Cretaceous to date, and the cuticle is amongst the oldest from angiosperms in the world. The few Cenomanian records of cuticle include Upchurch (1984, 1995) and Kvacek (1983, 1992), and for the Albian that of Crane *et al.* (1993).

The current knowledge of mid-Cretaceous angiosperms is based on pollen, flowers, and leaves, and includes several identifications of extant taxa. For instance, the Upper Albian Potomac Group of North America has yielded reproductive material regarded as of probable chloranthoid, hamamelididean, magnoliidean, platanoid, and rosidean affinities (Friis *et al.*, 1986; Crane *et al.*, 1986). The Cenomanian, or possibly late Albian Dakota Formation has yielded possible Magnoliales (Dilcher and Crane, 1984). These inferred affinities are at high taxonomic levels (but have still raised dispute, e. g. Hughes, 1994), nevertheless they may form a starting point for comparing fossil cuticle. Upchurch and Wolfe (1993) summarised the data from Cretaceous leaf fossils, including the latest Albian to middle Cenomanian period. Similar to the reproductive material

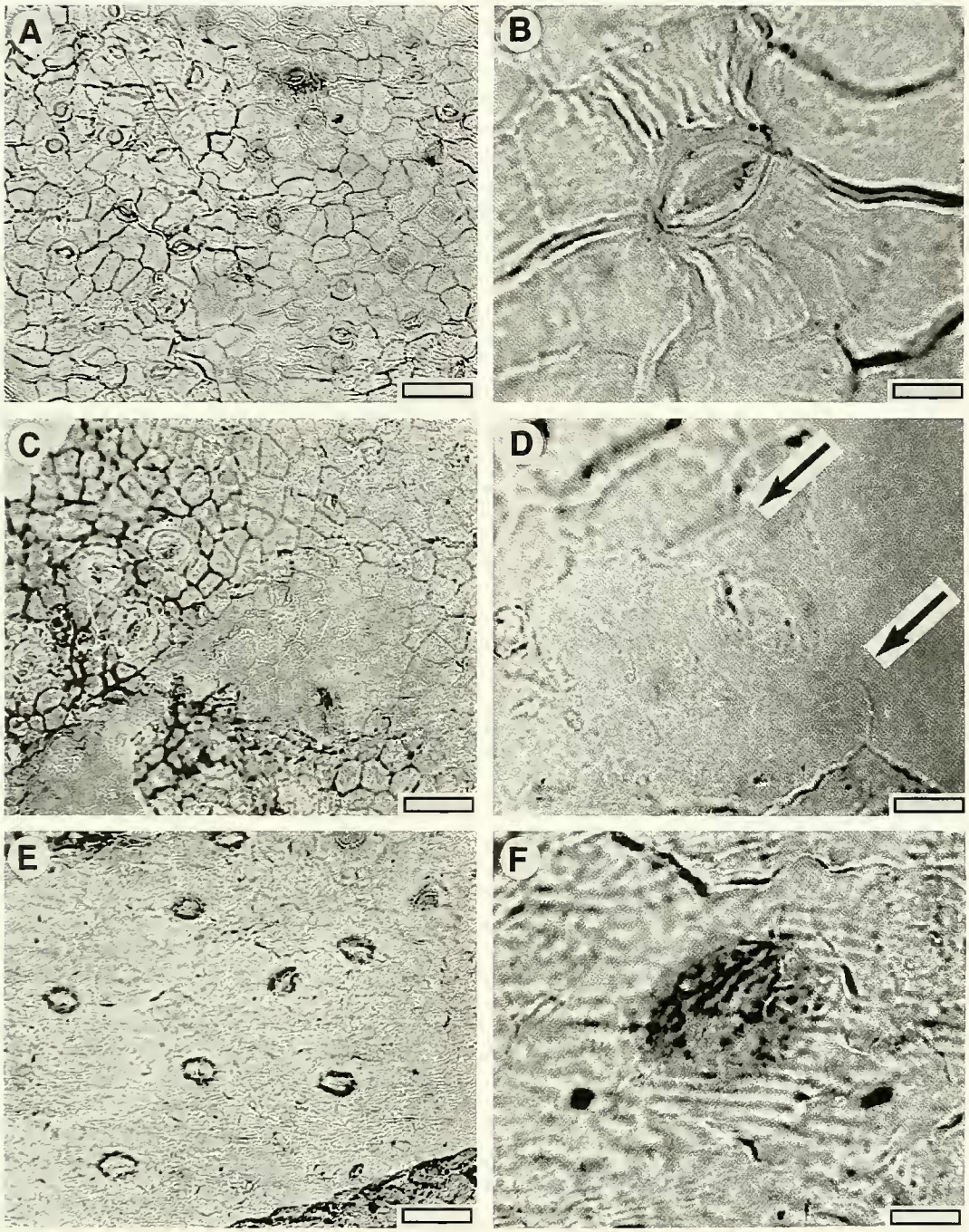

Figure 10. **A**, **B**. Dicotyledon sp. H, both SL987. **A**. Scale: 50 µm. **B**. Scale: 10 µm. **C**, **D**. Dicotyledon sp. I, both SL737. **C**. scale: 50 µm. **D**. Arrows point to opposite poles of a single stomate, scale: 10 µm. **E**, **F**. Angiosperm sp. J, both SL679. **E**. Scale: 50 µm. **F**. Scale: 10 µm.

the affinities included the Magnoliales, Laurales, Hamamelidales (aff. to Platanaceae) and the Rosidae. Thus, even at this relatively early stage, several of the major clades of angiosperms recognised by Chase *et al.* (1993), were present.

Despite having some indication of 'where to look' for the affinities of the Eromanga material, taxonomic placement is far from obvious. For one taxon (Dicotyledon sp. F) an affinity with the Chloranthaceae and Illiciales has been suggested, but for the others their identity remains completely unknown. This situation may result from a combination of inadequate material for comparison with extant plants as well as the likelihood that plants of this age had combinations of cuticle characters unknown today (e. g. Upchurch, 1984). Certainly none of the cuticle has any of the characteristic features of extant Australian families such as Lauraceae, Myrtaceae, or Proteaceae which are well known in the Tertiary record (and which would not be expected for this time). *Platanus* or extinct relatives were widespread in the mid-Cretaceous, including New Zealand (Pole, 1992), but none of the fossil cuticle is comparable to extant *Platanus* (documented by Brett, 1979). However, cuticle of Albian *Sapindopsis*, regarded as Platanaceae by Crane *et al.* (1993), compares favourably with Dicotyledon spp. A, F, and H in the presence of surface striations and form of the outer stomatal ledge. Curiously, where subsidiary cells can be seen, none of the Eromanga cuticle shows the paracytic subsidiary cell arrangement which is common in extant plant families often regarded as 'primitive', i. e. the 'paleoherbs' of Donoghue and Doyle (1989). However, Upchurch (1984) reported a plastic, variable condition of the subsidiary cell arrangement for Lower Cretaceous Potomac Group cuticles and suggested it to be an even more primitive style, although Baranova (1992) remarked that several extant taxa also show such plasticity. This plasticity is shown by Dicotyledon sp. D from the Eromanga. As for whole leaf form, the single larger leaf fragment of Dicotyledon sp. A is not comparable with any of the material illustrated by McLoughlin *et al.* (1995) from younger Winton Formation deposits, although its lobed form would not be out of place in their assemblage.

Distribution

All samples containing dicotyledonous fossils come from the Winton Formation, except three (MAC-11; MAN-34, 42), which came from the underlying Mackunda Formation.

Angiosperm cuticle was not found in sandy samples. This could be a result of its not surviving in that environment (i. e. fluvial abrasion destroyed the cuticle), or because physical distortion by sand grains during compaction may have rendered the cuticle unrecognisable. It may also be a real absence, suggesting angiosperms were typically absent along relatively high-energy sedimentary environments such as river margins or levees. However, the three Mackunda Formation samples come from marine sediments to where the fossils contained must have been transported by fluvial activity. Out of the 144 fossiliferous samples which were fine-grained or muddy, only 20 of them contained dicotyledonous remains and these were restricted to three of the seven cores; GSQ Machattie-1, GSQ Maneroo-1, and GSQ Thargominda-3 (Appendix 1). This suggests that, at least in the lower-energy floodplain environments, dicotyledons were either patchy in their distribution, or were relatively small plants, producing little biomass. They were evidently a small component of what was, on a regional scale, an overwhelmingly gymnosperm (mostly conifer) dominated flora (Pole, in prep.). Burger (1990), on the basis of palynological data, also concluded the angiosperms were patchily distributed. One sample (MAC-11) comes from a thin unit of Winton Formation bounded above and below by marine sediments which probably accumulated very close to sea level, perhaps as a delta lobe. The other samples are interpreted as accumulating essentially in an overbank/floodplain environment (see facies analysis of the Eromanga core by Fielding, 1992).

Although no dicotyledon fossils were recovered from coal, some samples were stratigraphically close. Sample THA-47 comes from a mud immediately below the prominent coal seam of Thargominda-3. Samples MAN 6, 8, 9, 11, 12 (closely spaced, all coming from a 4.5 m-thick muddy unit) are close to the prominent coal seam of Maneroo-1 but separated from it by a 3.5 m-thick sandy bed. The most reasonable assumption is that the angiosperms grew in clastic swamps, but growth on sandy levees or in coal swamps cannot be discounted. The plants were probably woody rather than herbaceous, as herbs are unlikely to become fossilised and their very delicate cuticle would not be expected to be preserved, or to survive the preparation process. Even so, some of the fossil cuticle is notably thin, consistent with understorey plants or deciduousness.

Summary

Latest Albian-earliest Cenomanian assemblages from the Eromanga Basin, Australia include sporadic fragments of dicotyledonous leaf cuticle, and rare semi-intact leaves. Ten types can be distinguished with the affinities of at least one possibly being with the Chloranthaceae and Illiciales.

Acknowledgements

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References

Alvin, K. L., 1974. Leaf anatomy of *Weichselia* based on fusainized material. *Palaeontology*, vol. 17, 587-598.

Baranova, M., 1992: Principles of comparative stomatographic studies of flowering plants. *The Botanical Review*, vol. 58, p. 49-99.

Brenner, G. J., 1996 : Evidence for the earliest stage of angiosperm pollen evolution: a paleoequatorial section from Israel. *In*, Taylor, D. W. and Hickey, L. J. *eds.*, *Flowering Plant Origin, Evolution and Phylogeny*, p. 91 - 115. Chapman and Hall, New York.

Brenner, G. H. and Bickoff, I., 1992: Palynology and age of the Lower Cretaceous basal Kurnub Group from the coastal plain to the northern Negev of Israel. *Palynology*, vol. 16, p. 137-185.

Brett, D. W., 1979: Ontogeny and classification of the stomatal complex of *Platanus* L. *Annals of Botany*, vol. 44, p. 249-251.

Burger, D., 1990: Early Cretaceous angiosperms from Queensland, Australia. Review of *Palaeobotany and Palynology*, vol. 65, p. 153-63.

Chase, M. W., Soltis, D. E., Olmstead, R. G., Morgan, D., Les, D. H., Mishler, B. D., Duvall, M. R., Price, R. A., Hillis, H. G., Qui, Y. -L., Kron, K. A., Rettig, J. H., Conti, E., Palmer, J. D., Manhart, J. R., Sytsma, K. J., Michaels, H. J., Kress, W. J., Karol, K. G., Clark, W. D., Hedren, M., Gaut, B. S., Jansen, R. K., Kim, K. -J., Wimpee, C. F., Smith, J. F., Furnier, G. R., Strauss, S. H., Xiang, Q. -Y., Plunkett, G. M., Soltis, P. S., Swensen, S., Williams, S. E., Gadek, P. A., Quinn, C. J., Equiarte, L. E., Goldenberg, E., Learn, G. H. Jr., Barnett, S. C. H., Graham, S. W., Dayanandan, S. and Albert, V. A., 1993: Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene rbcL. *Annals of the Missouri Botanical Garden*, 80, p. 528-580.

Cotthem, W. R. J., van, 1970a : Comparative morphological study of the stomata in the Filicopsida. *Bulletin Botanique National de Belgique*, 40, 81-239.

Cotthem, W. R. J., van, 1970b : A classification of stomatal types. *Botanical Journal of the Linnean Society,* vol. 63, p. 235-246.

Crane, P. R., Friis, E. M. and Pedersen, K. R., 1986 : Lower Cretaceous angiosperm flowers: Fossil evidence on early radiation of dicotyledons. *Science*, vol. 232, p. 852-854.

Crane, P. R., Pedersen, K. R., Friis, E. M. and Drinnan, A. N., 1993 : Early Cretaceous (Early to middle Albian) platanoid inflorescences associated with *Sapindopsis* leaves from the Potomac Group of eastern North America. *Systematic Botany*, 18, 328-344.

Dettmann, M. E. and Playford, G., 1969 : Palynology of the Australian Cretaceous: a review. *In*, Campbell, K. S. W. *ed.*, *Stratigraphy and Palaeontology- Essays in Honour of Dorothy Hill*, p. 174-210. Australian National University Press, Canberra.

Dettmann, M. E., Molnar, R. E., Douglas, J. G., Burger, D., Fielding, C., Clifford, H. T., Francis, J., Jell, P., Rich, T., Wade, M., Rich, P. V., Pledge, N., Kemp, A. and Rozefelds, A., 1992 : Australian Cretaceous terrestrial faunas and floras: biostratigraphic and biogeographic implications. *Cretaceous Research*, vol. 13, p. 207-262.

Dilcher, D. L. and Crane, P. R., 1984 : *Archaeanthus*: An early angiosperm from the Cenomanian of the Western Interior of North America. *Annals of the Missouri Botanical Garden,* vol. 71, p. 351-383.

Donoghue, M. J. and Doyle, J. A., 1989 : Phylogenetic analysis of angiosperms and the relationships of Hamamelidae. *In*, Crane, P. R. and Blackmore, S. *eds.*, *Evolution, Systematics, and Fossil History of the Hamamelidae, Vol 1, Introduction and 'Lower' Hamamelid*ae, p. 17 - 45. Clarendon Press, Oxford.

Douglas, J. G., 1965 : A Mesozoic dicotyledonous leaf from the Yangery No 1 bore Koroit, Victoria. *Mining and Geological Journal*, vol. 6, p. 64-7.

Douglas, J. G., 1994 : Cretaceous vegetation: the macrofossil record. *In*, Hill, R. S. *ed.*, *History of the Australian Vegetation. Cretaceous to Recent*, p. 171 - 188. Cambridge University Press, Cambridge.

Drinnan, A. N. and Chambers, T. C., 1986 : Flora of the Lower Cretaceous Koonwarra fossil bed (Korumburra Group) South Gippsland, Victoria. *Association of Australasian Palaeontologists Memoir*, vol. 3, p. 24-37.

Exon, N. F. and Senior, B. R., 1976 : The Cretaceous of the Eromanga and Surat Basins. *BMR Journal of Australian Geology and Geophysics*, vol. 1, p. 33-50.

Fielding, C. R., 1992 : A review of Cretaceous coal-bearing sequences in Australia. Controls on the distribution and quality of Cretaceous coals. *In*, McCabe, P. J. and Parrish, J. T. *eds.*, *Geological Society of America Special Paper* 267, 303-324.

Friis, E. M., Crane, P. R. and Pedersen, K. R., 1986 : Floral evidence for Cretaceous chloranthoid angiosperms. *Nature*, vol. 320, p. 163-164.

Harris, T. M. 1940. On some Jurassic specimens of *Sagenopteris*. *Annals and Magazine of Natural History* 6, 249-265.

Helby, R. J., Morgan, R. and Partridge, A. D., 1987 : A palynological zonation of the Australian Mesozoic. *Memoirs of the Association of Australasian Palaeontologists*, vol. 4, p. 1-94.

Hughes, N. F., 1994 : *The Enigma of Angiosperm Origins*, 303 p. Cambridge University Press, Cambridge.

Kvacek, Z., 1983 : Cuticular studies in angiosperms of the Bohemian Cenomanian. *Acta Palaeontologica Polonica*, vol. 28, p. 159-170.

Kvacek, J., 1992 : Leaf and fruit compressions from the Bohemian Cenomanian. *In*, Kovar-Eder, J. *ed.*, *Paleovegetational Development in Europe and Regions Relevant to its Palaeofloristic Evolution*, p. 301 - 305. Museum of Natural History, Vienna.

McLoughlin, S., Drinnan, A. N. and Rozefelds, A. C., 1995 : A Cenomanian flora from the Winton Formation, Eromanga Basin, Queensland, Australia. *Memoirs of the Queensland Museum*, vol. 38, p. 273-313.

Metcalfe, C. R., 1987 : *Anatomy of the Dicotyledons. Volume III. Magnoliales, Illiciales, and Laurales*, 224 p. Clarendon Press, Oxford.

Pole, M. S., 1992 : Cretaceous macrofloras of eastern Otago, New Zealand: Angiosperms. *Australian Journal of Botany*, vol. 40, p. 169-206.

Pole, M. S., 1999 : Latest Albian-earliest Cenomanian monocotyledonous leaves from Australia. *Botanical Journal of the Linnean Society*, vol. 129, p. 177-186.

Pole, M. S., and Douglas, J. G., 1999 : Bennettitales, Cycadales and Ginkgoales from the mid Cretaceous of the Eromanga Basin, Queensland, Australia. *Cretaceous Research*, vol. 20, p. 523-538

Sun, G., Dilcher, D. L., Zheng, S. and Zhou, Z., 1998 : In search of the first flower: a Jurassic angiosperm, *Archaefructus*, from northeast China. *Science*, vol. 282, p. 1692-1695.

Taylor, D. W. and Hickey, L. J., 1990 : An Aptian plant with attached leaves and flowers: implications for angiosperm

origin. *Science*, vol. 247, p. 702–704.

Upchurch, G. R., Jr, 1984 : Cuticle evolution in Early Cretaceous angiosperms from the Potomac Group of Virginia and Maryland. *Annals of the Missouri Botanical Garden*, vol. 71, p. 522–550.

Upchurch, G. R., Jr, 1995 : Dispersed angiosperm cuticles: Their history, preparation, and application to the rise of angiosperms in Cretaceous and Paleocene coals, southern western interior of North America. *International Journal of Coal Geology*, vol. 28, p. 161–227.

Upchurch, G. R., Jr. and Wolfe, J. A., 1993 : Cretaceous vegetation of the Western Interior and adjacent regions of North America. Geological Society of Canada Special Paper. *In*, Caldwell, W. G. E. and Kauffman, E. G. *eds.*, Evolution of the Western Interior Basin. *Geological Association of Canada Special Paper*, 39, p. 243–281.

Vine, R. R. and Day, R. W., 1965 : Nomenclature of the Rolling Downs Group, northern Eromanga Basin, Queensland. *Queensland Government Mining Journal September*, 66, p. 416–421.